

NEW CRETACEOUS AND TERTIARY CRABS (CRUSTACEA: BRACHYURA) FROM AUSTRALIA AND NEW ZEALAND

by M. F. GLAESSNER*

Summary

GLAESSNER, M. F. (1980) New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand, *Trans. R. Soc. S. Aust.* **104**(6), 171-192, 28 November, 1980.

From the Cretaceous of Australia and New Zealand three new genera of Brachyura, one new subgenus, and seven new species are described and one new family is proposed. Four new species from the Eocene are described, one from Australia and three from New Zealand, and changes in taxonomy and nomenclature are made. The new classification of the Brachyura (Guinot 1977) is applicable to the new material which contributes significantly to the clarification of taxonomic and phylogenetic relations at an early, critical stage in the evolution of the Brachyura. Modified Tethyan palaeobiogeographic relations of the Cretaceous and Palaeogene faunas are recognised.

Classification

A new classification of the Decapoda Brachyura proposed by Guinot (1977, 1978) is of particular interest to students of the evolution of these crustaceans. Based on generally sound and stated principles, and on a re-examination of a very large amount of zoological material as well as literature, it takes into consideration conclusions reached by palaeontologists, questioning some of these conclusions specifically. New material from Australia and New Zealand provides a suitable starting point for the task of answering some of the queries raised, and of testing the suitability of the proposed new system of the Decapoda Brachyura. The following tabulation places the new finds in the framework of Guinot's classification and indicates their age and occurrence.

Section Podotremata Guinot, 1977

Subsection Dromiacea de Haan, 1833

Superfamily Homolodromioidea Alcock, 1899

Family Prosopidae von Meyer, 1860

Oonoton woodsi nov. gen., nov. sp. Upper Albian, central Queensland and South Australia.

Subsection Archaeobrachyura Guinot, 1977

Superfamily Homoloidea White, 1847

Family Homolidae White, 1847

Homolopsis etheridgei (H. Woodward, 1892). Upper Albian, central Queensland.

Homolopsis spinulosa nov. sp. Upper Cenomanian, northern Australia.

Superfamily Raninoidea de Haan, 1833

Family Raninidae de Haan, 1833

Notopocorystes (Cretacorantina) exiguus nov. sp. Lower Cenomanian, Northern Australia.

Hemioon novozelandicum nov. sp. Upper Albian, New Zealand.

Ranilla pororariensis nov. sp. Upper Eocene, New Zealand.

Lyreidus waitakiensis nov. sp. Middle to Upper Eocene, New Zealand.

Superfamily Tymoloidea Alcock, 1896.

Family Torynommidae nov. fam.

Torynomma (Torynomma) flemingi nov. sp. Upper Senonian, New Zealand.

Torynomma (Paratorynomma) dentatum nov. subgen., nov. sp. Upper Cenomanian—Lower Turonian, northern Australia.

Dioratiopus salebroxus Woods, 1953 Upper Albian, Queensland and South Australia.

Dioratiopus sp. Upper Cenomanian, northern Australia.

?*Eodorippe spedeni* nov. gen., nov. sp. Upper Senonian, New Zealand.

Section Heterotremata Guinot, 1977.

Superfamily Portunoidae Rafinesque, 1815.

Family Portunidae Dana, 1852.

Subfamily Psammocarcininae Beurlen, 1930.

Rhachiosoma granulifera (Glaessner, 1960) Upper Eocene, New Zealand.

Family uncertain.

Pororaria eocenica nov. gen., nov. sp. Upper Eocene, New Zealand.

Superfamily Xanthoidea McLeay, 1838.

Family Panopeidae Ortmann, 1893.

Panopeus whittegensis nov. sp. Upper Eocene, South Australia.

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The most distinctive innovation affecting the classification of the Brachyura discussed here

is the demotion of the "Section Dromiacea" which has dominated considerations on the origin and evolution of the Mesozoic Brachyura for more than a century. Guinot recognises three sections: the Podotremata, Heterotremata and Thoracotremata, named according to the position of the gonopores. This looks rather like a single-character classification to which I objected (Glaessner 1969) when the peditrema-sternitrema distinction (Bouvier 1897) was used by Gordon (1963) to remove the former group from the Brachyura. However, Guinot (1978) has amply demonstrated that it is a distinction by grades, the use of which she finds inevitable for taxa of high rank while following to some extent "pré-occupations d'ordre cladistique" for lower-rank taxa. This taxonomic innovation involves recognition of two subsections of the Podotremata, the Dromiacea and the Archaeobrachyura. The former comprise the Superfamilies Homolodromioidea and Dromioidea, the latter the Homoloidea, Raninoidea and Tymoloidea. This classification is significant for the present investigation. There is ample morphological evidence for close links between the Tymoloidea and the Homoloidea. The Dromioidea (Families Dromiidae and Dynomenidae) have taken a different evolutionary path. With reference to the descriptions and discussions which follow, it is sufficient to note here that *Homolopsis* and *Torynomma* (with related genera) are morphologically close and, as Wright & Collins (1972) have indicated, appear to have had Prosopidae, hence Homolodromioidea, as ancestors in Jurassic time. The Dromioidea differ significantly from this group in many morphological, embryological and ethological characters. For the question of the evolution and systematic position of the Raninoidea there is no significant new material under discussion here (see Förster 1968, Števčić 1973). I had previously (Glaessner 1969) assigned the Tymolinae to the Dorippidae, following the latest comprehensive classification available at that time (Balss 1957). This is now unnecessary and unacceptable, since Guinot's work has shown that the oxy-stomatous condition (which has to do with the direction of the inhalent and exhalent currents of water under the carapace) was reached independently by very different groups of crabs. Thus there is no justification for retaining the artificial taxon Oxystomata. With this demonstration most of the major classification of the Brachyura, of long stand-

ing but often questioned, had to be abandoned. The origin of all or some of the older Heterotremata (Dorippoidea, Calappoidea, Corystoidea (=Cancriformia), Portunoidea and (questionably) Xanthoidea (see Wright & Collins 1972) from Cretaceous Tymoloidea or their ancestors is possible or even probable, but these investigations would lead beyond the limits set by the material here described.

Summary of stratigraphic distribution

(New Zealand species marked with asterisk)
Upper Albian: *Oonoton woodsi*, *Homolopsis etheridgei*, **Hemioon novozelandicum*, *Dioratiopus salebrosus*.

Lower Cenomanian: *Notopocorystes (Cretacoranina) exiguus*.

Upper Cenomanian: *Homolopsis spinulosa*, *D.* sp.

Upper Cenomanian to Lower Turonian: *Torynomma (Paratorynomma) dentatum*.

Campanian-Maastrichtian: **Torynomma (T.) flemingi*, **Eodorippe spedeni*.

Middle to Upper Eocene: **Lyreidus waitakiensis*.

Upper Eocene: **Ranilia pororariensis*, **Rhachiosoma granulifera*, **Pororaria eocenia*, *Panopeus whittenerensis*.

Remarks on palaeobiogeography

While we know only a small sample of the Brachyura of the Cretaceous and Eocene of Australia and New Zealand, theoretical conclusions are unwarranted. It is worth noting that known relations are dominantly with European genera. *Homolopsis*, *Notopocorystes* (which is almost cosmopolitan), *Hemioon*, *Dioratiopus*, *Rhachiosoma* and *Panopeus* (which is also Atlantic) are well known from Europe. As far as the Australasian region is concerned, the origin of these genera can be considered as Tethyan. *Torynomma* has its range extended from Queensland to the north of Australia in the Cenomanian, and to New Zealand in the Campanian-Maastrichtian. Its close relative *Dioratiopus*, a genus shown to include many European species, is recorded, in addition to Queensland, from northern South Australia and from Melville Island north of Darwin. The undescribed macruran and thalassinacean decapods from the Cenomanian of the island (*Paraclytia*, *Hoploparia*, *Trachysoma* and *Protocallianassa*) are well known from the European Upper Cretaceous. The Tethyan

relations of the Brachyura from Bathurst Island are in agreement with the character of its Cenomanian ammonite fauna (Wright 1963). *Eodorippe* from the Upper Senonian of New Zealand is endemic, and the endemic Recent *Nectocarcinus* may have had an ancestor dating back to the Eocene in the same region, the new genus *Porofaria*.

Descriptions

Family Prosopidae

Oonoton nov. gen.

Derivation of name: From Greek *oon*: egg, *noton*: back, with reference to shape.

Diagnosis: Carapace ovoid, without sharp lateral margins, posterior margin short, rostrum triangular, truncated, with transverse groove and row of granules at base; eye sockets close-set with strong supra- and infraorbital spines; mesogastric lobe long and narrow, urogastric lobe indistinct, carapace surface granulated.

I had intended to assign this fossil to *Vectis* Withers, 1946, but Mr C. W. Wright kindly informed me in July 1980 of his disagreement with such an extension of this taxon. I accept his view that the differences between the Australian crab and the three English species are of generic significance. They leave *Oonoton* closer to *Vectis* than to other genera.

Oonoton woodsii nov. sp.

Derivation of name: After Dr J. T. Woods, Director of Mines, Queensland who has made valuable contributions to the knowledge of Cretaceous Decapoda from Queensland.

Material: 1. Holotype—An almost complete carapace, Qld Mus, F 2876. 2. One fragmentary carapace, Geological Survey of South Australia No. Cr 1.

Localities: 1. Currane Station, 16 km N of Dartmouth, central Queensland. 2. 14 km W of Mt Dutton (Loc. 17, Map Sheet 5/571, see Bull 40, Geol. Survey S. Aust. p. 44).

Preservation: The Queensland specimen is well preserved in a smooth, round, concretionary nodule, similar to those which contain other crabs from the Queensland Cretaceous. The South Australian specimen consists of internal moulds of two angular fragments of the posterior portion of the carapace, partly overlapping, in a concretion containing numerous mollusca. The mode of preservation and the association suggest that the carapace may have been broken by a predator, probably a belemnite or an ammonite.

Age: Upper Albian, Tambo Formation of Queensland and Oodnadatta Formation of South Australia.

Description: Carapace of holotype ovoid, 27 mm long, 22.4 mm wide, about 8.5 mm high. Convex antero- and posterolateral margins of about equal length; lateral margins almost parallel, longitudinal and transverse profiles of carapace (Figs. 1A, B) strongly and smoothly convex. Apically truncated triangular rostral plate directed forward, set off from anterior slope of carapace by transverse groove and row of granules in front of mesogastric region. Eye sockets deep and small, with strong, conical, supraorbital and long infraorbital spines which are twice as long and set below. Anterolateral outlines diverge to crossing points of cervical grooves and widen only slightly to metabranchial regions. Posterior margin apparently not as long as in *Vectis*. Regions well marked by smooth, shallow furrows. Mesogastric lobe not subdivided. Almost entire surface of carapace fairly evenly covered with large granules. Additional small tubercles on metabranchial regions, and 5 distinctive, larger, granulate elevations. Two are symmetrically arranged on mesogastric lobe, 2 on metagastric lobe which is divided by deep median furrow, 1 on cardiac lobe. Its distance from posterior margin $\frac{1}{2}$ that from base of rostrum. Cardiac grades into narrow intestinal lobe.

This species differs from two Aptian and one Albian species of *Vectis* previously described from England in details of shape and surface sculpture. It has all the significant characters of their carapace regions but they are not as tumid and therefore less conspicuous in the new species. The characters which are preserved in the smaller specimen from South Australia do not differ from those of the holotype from Queensland.

Family Homolidae

Homolopsis Bell, 1863

Homolopsis etheridgei (Woodward, 1892)

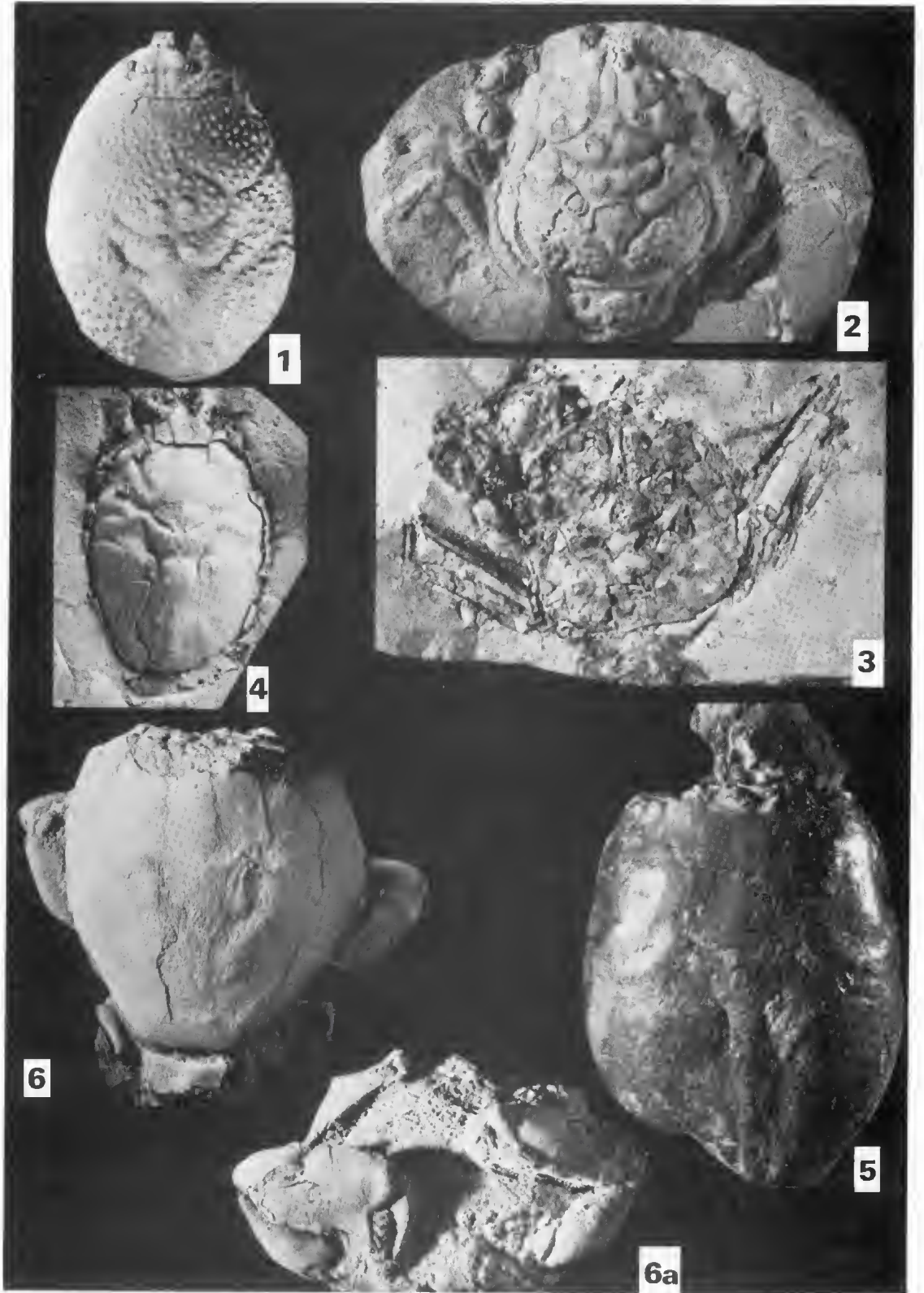
FIG. 2

Prosopon etheridgei Woodward 1892, p. 301, pl. 4; Etheridge 1917, p. 5, pl. 1, fig. 1-4.

Homolopsis etheridgei: Van Straelen, 1928, p. 619; Woods, 1953, p. 50, pl. 2, fig. 1-3, text fig. 1.

Material: One almost complete specimen (P22945).

Locality: "Currane", 14 km N of Dartmouth, central Queensland. Coll. J. T. Woods 1955.



Age: Upper Albian, Tambo Formation.

Remarks: This specimen is figured here for comparison for completeness of the record of currently known Australian Cretaceous crabs. It has a significantly more convex carapace than the species figured by Wright & Collins (1972) and its upper surface is certainly not "more or less flat" as their generic diagnosis of *Homolopsis* requires. It may be appropriate to place the Australian species in a new sub-genus unless species with traditional shape characters exist.

Homolopsis spinulosa nov. sp.

FIG. 3, 3A

Holotype material: One small, somewhat crushed specimen with counterpart, P22934. Coll. B. Daily 1954.

Locality: South coast of Melville Island, N.T., about 10 km NW of Cape Gambier.

Age: Upper Cenomanian, Bathurst Island Formation, about 8 m above "Tapara Bed".

Preservation: Preserved in a slightly weathered yellowish clay is the cephalothorax with two abdominal somites, the left cheliped and parts of all other pereopods. Ferruginised and affected by compaction and weathering; most of the carapace margins defective. Artificial moulds of the counterpart show details not recognisable in the damaged specimen.

Description: Carapace about 12 mm long and 14 mm wide, fronto-orbital width about 8 mm; anterolateral margins diverging, posterolateral margins slightly converging; posterior margin about 5 mm long, curved, with granulated edge. Ornamentation consists of distinct, granulated tubercles; at least 1 epigastric, 2 protogastric, 1 hepatic, 2 epibranchial and 3 metabranchial tubercles present on each side and also metagastric and cardiac tubercle-bearing ridges. Surface finely and evenly granulated. Left cheliped short and robust, with a spinose carpus; P2 and P3 strong, long, with spinose edges, the P4 appear near the posterolateral angles of the carapace, thin, smooth P5 near the base of the abdomen. First two abdominal somites about 5 mm wide, rectangular in outline, subequal, about 0.75 mm long, with two longitudinal shallow

grooves and elevations on a blunt transverse ridge on each somite. Abdomen extending horizontally backward.

This species appears to differ from other species of *Homolopsis* and also from "*Glaessneria*" *depressa* (Carter) as described by Wright & Collins (1972) mainly in details of ornamentation. The *linea homolicea* is partly visible and partly obscured by compression and fracturing of the only known carapace.

Family Raninidae

Notopocorystes M'Coy, 1849

Notopocorystes (Cretacorantina) exiguus

nov. sp.

FIG. 4, 4A

Derivation of name: From Latin *exiguus*: small.

Material: One carapace, with counterpart, in a bore core. Forwarded by Mr P. Bollen. P22929.

Locality: Bathurst Island Oil Development Well No. 2, about 4 km N of the mouth of Pipanyamili Creek, about 30 km W of Bathurst Island Mission, Core from 280 m depth.

Age: Lower Cenomanian, Bathurst Island Formation, grey clay.

Preservation: Carapace undistorted but most of the extremely fragile shell attached to the counterpart and anterolateral and orbital margins damaged.

Description: Carapace ovoid, 15 mm long, 10 mm wide. Width of the fronto-orbital margin about 5.4 mm. Carapace gently convex transversely and longitudinally, greatest height in the centre. Median ridge very faint. Rostrum bifid, medially grooved, slightly deflexed. Two supraorbital fissures. Extraorbital teeth could not have been large. Only 3 very weak lateral tubercles, 1 hepatic, 1 epibranchial and 1 extremely weak mesobranchial, followed by a finely granulated ridge along posterolateral margin. Posterior margin about 6 mm long but not well preserved. Cervical furrow, gently curved, runs from a notch in front of the epibranchial tubercle in a forwardly convex curve, then follows a sinuous course to distinct posterior gastric pits. Epibranchial furrows short,

Fig. 1. *Oonotus woodsi* nov. sp. x2.

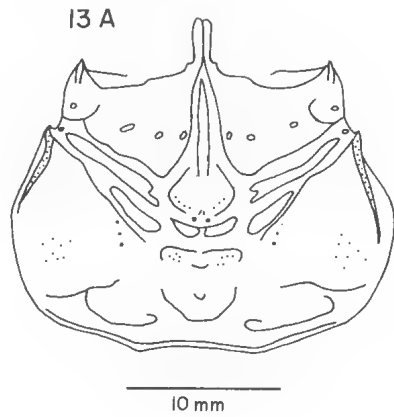
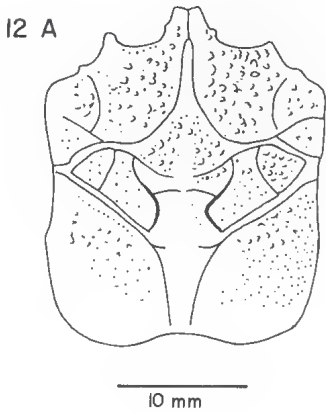
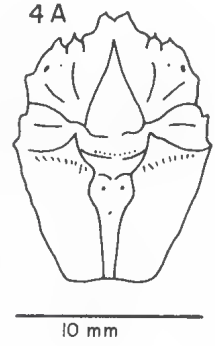
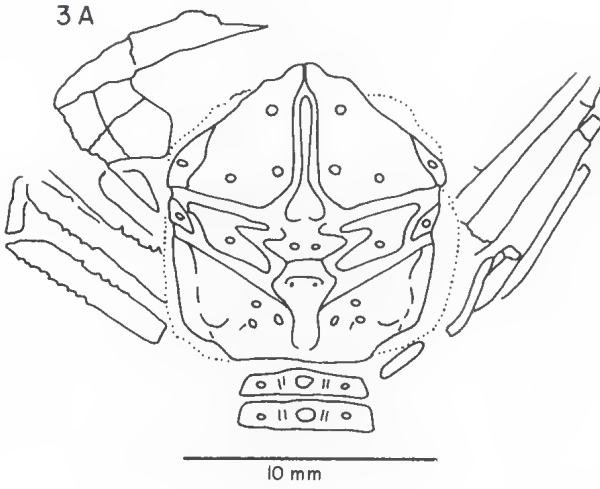
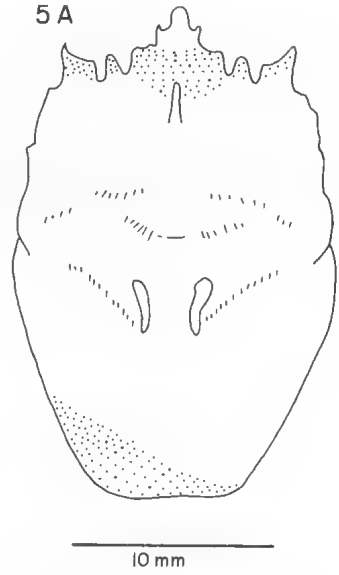
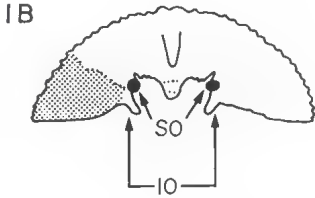
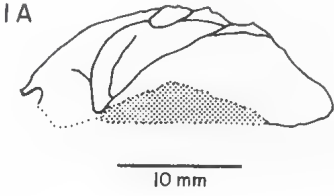
Fig. 2. *Homolopsis etheridgei* (H. Woodward).

Fig. 3. *Homolopsis spinulosus* nov. sp. x3.

Fig. 4. *Notopocorystes (Cretacorantina) exiguus* nov. sp. x3.

Fig. 5. *Hemiaon novozelandicum* nov. sp. x3.

Fig. 6. 6a. *Ranilla pororariensis* nov. sp. x2, a—dorsal view, b—ventral view.



transverse, do not reach the cervical groove. Branchiocardiac furrows more distinct, particularly their posterior edges, merging with the deep epimeral grooves. Epimeral and posterior gastric muscle attachments well marked on the inside of the carapace. The described furrows, together with hepatic and weaker mesogastric furrows form a peculiar radiating pattern on the outer surface which is finely pitted and granulated. Two elongate, tuberculate protuberances on the anterolateral parts of the carapace; outer ones smaller and prominent on the hepatic lobes, inner ones situated on outer portions of the protogastric lobes which are partly separated from the main parts by shallow grooves.

Remarks: The weak marginal spines and the surface sculpture place this species in the subgenus *Cretacorantina* Merlín, 1941. It does not appear to be particularly close to any of its known species but detailed comparison must await the discovery of further specimens.

Hemloon Bell, 1863

Hemloon novozelandicum nov. sp.

FIG. 5, 5A

Holotype material. One specimen in a hard concretion. Geological Survey of New Zealand GS11845.

Locality: Swale Stream, Coverham, South Island of New Zealand (P30/f. 56).

Age: Latest Albian. Lower part of Swale Siltstone, Ngaterian local Stage. Dr J. Speden (in litt, 1977) suggests Lower Ngaterian, from near the base of the *Worthoceras parvum* Assemblage Zone of Henderson (1973).

Preservation: Cephalothorax preserved as an internal mould, off central position, in a very hard concretion which does not split evenly. Sternum not visible but fragments of legs and chelae preserved in slightly displaced positions and much of the inside of the carapace shell is visible. Although the rostrum remained in the counterpart matrix when the concretion was split, it was possible to extract its tip and rejoin it so that the length of the rostrum could be determined (Fig. 5A).

Description: Cephalothorax ovoid, flattened longitudinally and convex transversely, lateral margin discontinuous, weakly developed. Two weak anterolateral spines and an acicular extraorbital spine with granulated surface. Orbits large, well marked, with two supra-orbital fissures and a stout supraorbital tooth. Rostrum about 3 mm long, straight, with two lateral basal spines. Markings on carapace surface very weak. Internal mould shows median parts of cervical groove curving laterally from posterior gastric pits, the anterior tip of the mesogastric lobe, epimeral grooves, and relies of the branchiocardiac grooves. Narrow median ridge marking cardiac and intestinal lobes. Strong muscle pits in the hepatic regions. Surface of carapace finely pitted where it can be seen. Posterolateral margins granulate. The greatest width (16.5 mm) is found between posterolateral margins which are separated from the anterolateral margins by a slight constriction behind the second anterolateral teeth. Marked, narrow, pterygostomial ridge and a wide depression along brachio-stegite. Posterior margin missing. Carapace was at least 25 mm long, greatest width is at about 0.6 of its length.

Remarks: The new species differs from *H. elongatum* (A. Milne Edwards 1862) in the shape of the carapace, the weak lateral teeth and the absence of surface tubercles. *H. circumulator* Wright and Collins 1972 also has strong anterolateral spines and convergent lateral margins on the posterior half of the carapace. These differences remove the new species further from *Raninella* as revised by Wright & Collins than those considered by these authors. It differs more in shape and carapace sculpture from *Notopocorystes* (*Cretacorantina*).

Raullia H. Milne Edwards, 1837

Ranilia porocariensis nov. sp.

FIG. 6, 6a

Holotype material. One carapace, slightly distorted by flattening, most of fronto-orbital margin missing. Chelipeds and some displaced or broken pereopods preserved, sternum not

Fig. 1A. *Oonotus woodsi* nov. sp., left side view; 1B front view. SO—position of supraorbital spine, IO—infraorbital spine. Stippled parts of carapace are missing or concealed.

Fig. 3A. *Homolopsis spinulosus* nov. sp. Partial reconstruction. Dotted line indicates outline of crushed carapace.

Fig. 4A. *Notopocorystes* (*Cretacorantina*) *exiguus* nov. sp. Reconstruction of carapace showing pattern as seen on inner surface.

Fig. 5A. *Hemloon novozelandicum* nov. sp. Reconstruction of carapace. Stippled parts are missing.

Fig. 12A. *Diorulopus salebrosus* Woods. Reconstruction of carapace.

Fig. 13A. *Eodorippe spedeni* nov. sp. Diagrammatic reconstruction of carapace pattern and rostrum.

visible, first abdominal somite preserved, Canterbury Museum, Christchurch, New Zealand, No. zfc 7. Coll. R. S. Allen, Feb. 1935.

Locality: Coastal cliffs at Pororari, 2.4 km N of Punakaiki. Sheet No. S37/723. Grid ref. C852318.

Age: Kaiatan—Runangan, Late Eocene.

Description: Carapace ovoid, strongly convex transversely; height about equal to half the width; gently convex longitudinally. Distance between the extraorbital and lateral acicular teeth equals that between lateral teeth and point of greatest width which is at the level of the postero-gastric pits; distance from this point to posterior margin almost 3 times longer. Posteriorly convergent posterolateral margins marked by a smooth ridge which is convex in dorsal view for first half of their length, then straight. Posterior margin straight. A very faint median ridge on posterior half of carapace. Two supraorbital fissures separated by a small tooth, only base preserved. Surface of carapace uniformly pitted, marked only by weak epimeral muscle impressions. First abdominal segment trapezoidal, surface pitted but otherwise smooth. Propodus of cheliped has sharp, denticulated upper edge and strongly deflexed fixed finger. Dactylus gently curved, with narrow dorsal groove between two ridges.

Remarks: The new species differs in shape and ornamentation and in the deflexed fixed finger from living species. It is distinguished by the weak longitudinal ridge and the anterolateral teeth from the Eocene *R.* ("*Notopella*") *vareolata* (Lorenthey). Further specimens in a better state of preservation and preparation are required for complete description and comparison.

Lyreidus de Haan, 1841

Lyreidus waitakiensis nov. sp.

FIG. 7, 7a

Holotype material: One carapace, front mostly missing, Canterbury Museum, Christchurch, New Zealand, No. zfc 30.

Locality: Black Point, Waitaki Valley, S127/368, Grid reference c 364 916. Another less well preserved specimen (Canterbury

Museum, No. zfc 8, coll. R. S. Allen Feb. 1935, from coastal cliffs at Pororari, 2.4 km N of Punakaiki) probably belongs to this species.

Age: Middle to Upper Eocene, Tapui glauconitic sandstone, Bartonian Stage. This may be the oldest known species of *Lyreidus*. The other specimen, tentatively named *L.* cf. *waitakiensis*, is from the Upper Eocene, Kaiatan-Runangan.

Preservation: Inner layer and parts of outer of shell of holotype present. Complete branchiostegites, part of the left antennal base and small, displaced sternal fragments also preserved.

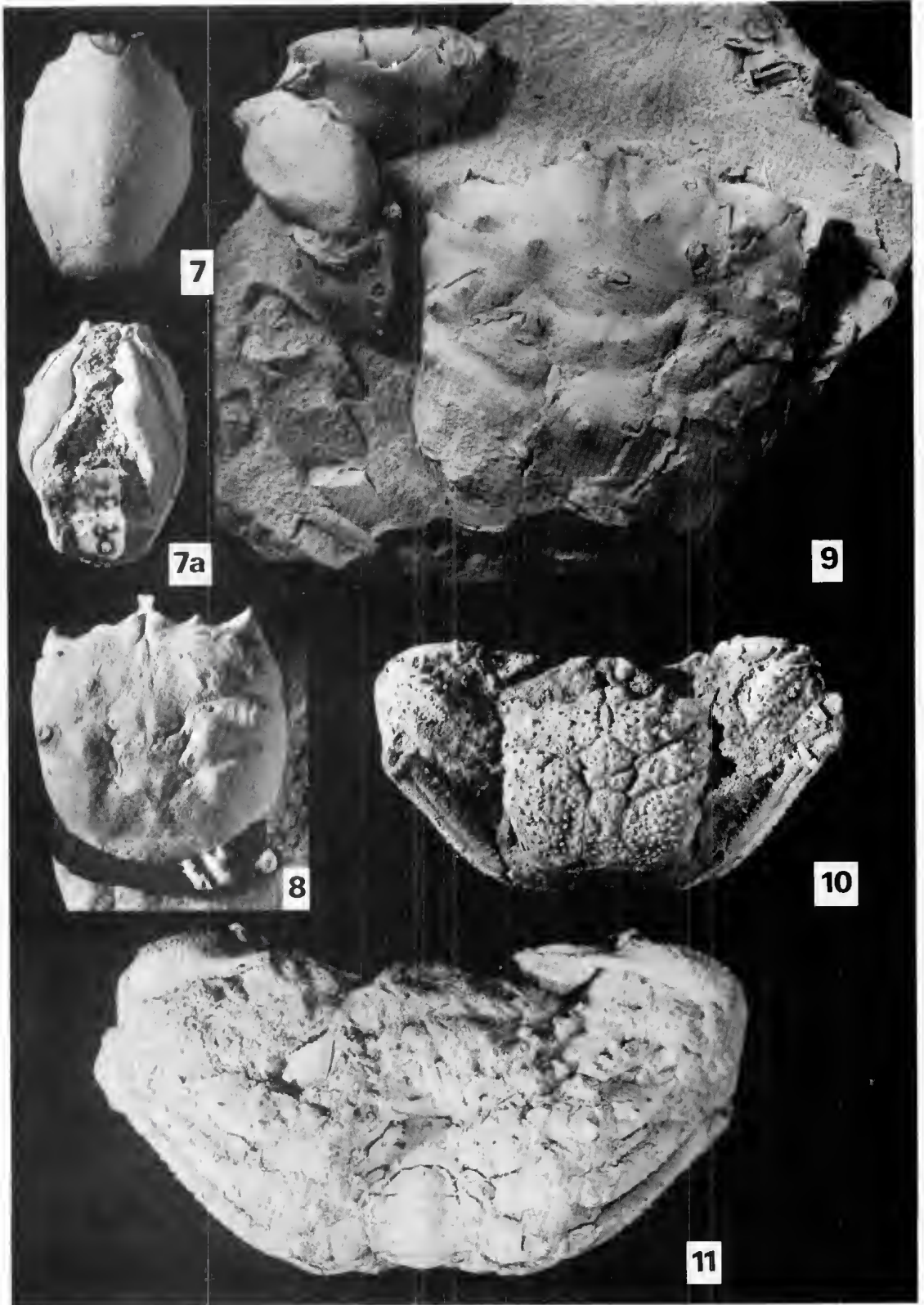
Description: Carapace ovate; fronto-orbital region 6.5 mm wide, with 2 supraorbital fissures; anterolateral margins diverging from the extraorbital to obliquely pointed lateral teeth. Distance between their tips is about 3.5 mm, equal to greatest width of carapace measured about 3 mm behind them. Anterolateral margins rounded, a bluntly conical tooth on each side halfway between extraorbital and lateral teeth. A blunt edge extends a short distance behind the lateral teeth, replaced from below by a distinct, sharp, posterolateral ridge with small granules. Posterolateral margins converge to arcuate posterior margin which equals fronto-orbital margin in length. Carapace strongly convex transversely, gently convex longitudinally; pterygostomial regions inflated. Pleural suture sinuous anteriorly, parallel to lateral margins and a short distance below them. Surface of carapace shows postero-gastric pits 2 mm behind level of the lateral teeth, and weak epimeral attractor muscle markings some distance behind them; smooth but may have been faintly pitted and weakly granulated in some places. Two weak epigastric tubercles. Pterygostomial regions granulated. Orbits only slightly oblique in frontal view, with small infraorbital spines separated by fissures from extraorbital teeth. Antennal base has lateral, longitudinal, granulated ridge with channel along its outer side, between it and edge of carapace; it may lead to the proximal side of the infraorbital tooth.

Remarks: This species can be distinguished by its ovoid shape and its ornamentation. The

Fig. 7, 7a. *Lyreidus waitakiensis* nov. sp. x2. a—dorsal view, b—ventral view.

Fig. 8. *Torynomma quadratum* Woods. Plaster cast of holotype, x2. Rostrum drawn from another specimen.

Figs. 10, 11. *Torynomma (Paratorynomma) dentatum* nov. sp. 10—holotype, x1.5, dorsal view, 11—paratype P 22931, x2. Ventral view with anterior sternum and abdomen of ♀ and pereopods.



shape of the carapace appears to be of slightly more generalised raninid type than in the Miocene and living species which are anteriorly more sharply narrowed and strongly elongated.

Family *Torynommidae* nov. fam.

The genus *Torynomma* was originally placed in the family "Prosoponidae" (*recte* Prosopidae), together with *Dioratiopus* (Woods 1953, p. 52). These genera have hardly more than a few primitive (plesiomorphic) characters in common with the Prosopidae but they do not have any of the distinctive, diverse developments of shape of the carapace and rostrum or the dominance of the transverse carapace grooves which characterise this family. The placing of *Torynomma*, *Dioratiopus* and other extinct genera in the subfamily Tymolinae Aleock, 1896, as proposed by Glaessner (1969) is considered inappropriate by Wright & Collins (1972). Concerning the placing of the Tymolinae in the Dorippidae, Gordon (1963, p.56) stated: "Certainly the so-called Tymolinae with sternal furrows and coxal genital pores should not be placed in the same family as the dorippids without sternal furrows and with the genital openings of the female sternal". I rejected (Glaessner 1969, p.R440) Gordon's further conclusion that it seems logical to exclude all peditreme crabs "from the Brachyura, restricting the term to the vast majority of crabs with the female genital openings sternal". I noted that the Dromiacea, Raninidae and Tymolinae which have coxal female gonopores are "exceptional" and that their separation "on the basis of an obviously primitive character is an extreme application of 'horizontal classification' which is not acceptable, particularly as the steps in the evolution from the primitive peditreme to the advanced sternitreme condition have not yet been studied on fossil material". Hence I followed the earlier systematists and Balss (1957) who placed the Tymolinae in the family Dorippidae. Guinot's work (1977, 1978) has now removed the traditional major subdivisions of the Brachyura such as the Oxystomata, which had been hampering the development of systematics in this group since the middle of the last century. It showed that Gordon had been remarkably far-sighted in recognising the peditreme-sternitreme evolutionary transition as a fundamental change which can provide a firmer basis for the major classification of the Brachyura than the diagnostic characters of the traditional major taxa. How-

ever, this reclassification also rejected Gordon's "logical conclusion" that the peditreme crabs are not Brachyura. The steps in the evolution from the peditreme to the sternitreme grade (Guinot's Sections Podotremata and Heterotremata) are now better documented both in living and in fossil forms including those described or reconsidered here. Earlier erroneous classifications on family and subfamily level (Balss, Glaessner) must now be corrected in the light of these data. However, they are still incomplete as far as palaeontological material is concerned.

Wright & Collins (1972) assigned to the family Cymonomidae (erroneously ascribed to Ihle 1916 but actually named by Bouvier 1897 as Cymonomae) the fossil genera *Glaessneria* Wright & Collins, 1972 (re-named *Glaessnerella* in 1975) and *Dioratiopus* J. T. Woods, 1953, considering them as "closely allied". It will be shown below that they are synonymous. Also included was *Mithracites* Gould, 1859, but *Withersella* Wright & Collins, 1972 and *Binkhorstia* Noetling, 1881 were omitted and rather unconvincingly placed in the Carcineretidae. The fossil genera included by Wright & Collins range from Lower Aptian to Cenomanian; *Binkhorstia* is Maastrichtian. I have included in the subfamily Tymolinae the Upper Eocene *Falconoplax* Van Straelen, 1933. Its sternum is flat and wide, with a deep abdominal depression and well marked sternal grooves between sternites 4-8 and a deep furrow in the anterior portion of sternite 8 of the female. On the criteria used by Guinot for suprageneric taxa it would seem necessary to exclude this genus. The Tymoloidea, according to Guinot (1978) with one family Tymolidae, comprise 2 subfamilies Tymolinae Aleock, 1896 and Cymonominae Bouvier, 1897, in which the living genera *Cymopolus* A. Milne Edwards, 1880 and *Cymonomus* A. Milne Edwards, 1880 are included. They have a square, rugose, granulate or spinose carapace, a narrow, triangular, pointed rostrum, reduced eyes or fixed eyestalks without cornea, in addition to other characters which are not discerned in fossils. They live in deeper water, from 134 to 1269 m (Ihle 1916) and some are abyssal. It seems undesirable to attach a varied and widely distributed group of shallow-water crabs with a spatulate rostrum, large, apparently normal eyes and a tymoline sternum to a minor group of small deep-water crabs which, as we shall see, are not their only descendants. I propose to

separate the Cretaceous genera *Torynomma*, *Dioratiopus*, *Mithracites*, *Binkhorstia* and provisionally *Eodorippe* as a new family Torynomidae which appears to be a more "natural" taxon for them in the sense that its recognition helps the discussion of its relations. Those with Homoloidea and Prosopidae remain to be clarified after further studies of their Jurassic representatives and, if possible, of the Hauterivian "*Glaessneria*" *signouxi* (Van Straelen) mentioned by Wright & Collins (1972, p.35). However, this single, fragmentary specimen, of uncertain provenance, can no longer be found (R. Förster, pers. comm. July 1980). Relations to Dromiidae and Dynomenidae with which their living descendants have been compared do not appear to be close. The Torynomidae are probably ancestral to Tymolidae (Cymoninae+Tymolinae) and possibly also Dorippidae and Palicidae, similar to relations depicted in Bouvier's phylogenetic diagram (Bouvier 1897, A. Milne Edwards 1902, p.106) where their place is taken by unspecified "Dynoméniens".

Diagnosis of the family Torynomidae: Carapace square, rectangular or pentagonal in outline, convex, front spatulate, projecting, not strongly deflexed; regions well marked by grooves including the branchiocardiac; lateral margins not sharp, side walls steep, eyes well developed, retractable into shallow orbits. Sternum triangular anteriorly, oval in outline posteriorly, with the last sternites vertical and chevron-shaped. It resembles the sternum of the Tymolinae and Homolidae rather than the configuration of the sternum in the Dromiacea. Where known, the gonopores are coxal (peditreme). Chelipeds subequal, second and third pereopods long and strong, fourth and fifth (or the fifth only) in dorsal position and much reduced. Abdomen with first somites exposed dorsally. Cretaceous (Aptian to Maastrichtian).

Torynomma Woods, 1953

***Torynomma (Torynomma) flemingi* nov. sp.**
FIG. 9

Derivation of name: After Sir Charles Fleming F.R.S., who has made outstanding contributions to the palaeontological knowledge of New Zealand.

Holotype material: Victoria University, Wellington, No. VA122.

Locality: Koutu Point, Hokianga Harbour (Loc. V2114). New Zealand.

Age: Upper Senonian-Maastrichtian, Mata Series.

Description: Carapace slightly convex, approximately square in general outline, about 30 mm long and wide. Anterolateral margins almost straight, posterolateral margins which are damaged were slightly convex, width of carapace across antero- and posterolateral margins was about equal but reduced about middle of its length. Orbits large, very shallow; orbital margin straight, transverse. Extra-orbital tooth conical, pointed, directed diagonally forward, outward and upward. Regions and lobes well marked. One small tubercle on anterior mesogastric lobe, one pointed tubercle on its centre. Posterior gastric pits clearly marked. All other spinose tubercles arranged symmetrically: 1 on each side of the hepatic, metagastric and cardiac lobes, 2 on each protogastric and epibranchial lobe. Branchial regions granulate. Carpus and merus of the cheliped have sharp dorsal ridges. Chelipeds robust, subequal. Fourth and fifth pereopods very weak.

Remarks: This species differs from *T. quadratum* Woods (Fig. 8) in its size and the shape of the carapace which is flatter and has a squarish outline. The spines on the surface are more numerous and much more prominent.

***Paratorynomma* nov. subgen.**

Type species *Torynomma (P.) dentatum*
nov. sp.

This subgenus differs from *Torynomma* Woods in its flatter and wider carapace with a less deflexed rostrum and a strongly and evenly granulated surface. Its most obvious difference is seen in the prominent anterolateral extra-orbital teeth which are triangular, directed forward and outward, and mark the greatest width of the carapace. The chelae are more slender and elongate and the chelipeds are longer. It differs from *Dioratiopus* by its almost straight fronto-orbital margin and slightly converging posterolateral margins but resembles it in its granulate surface sculpture and elongate chelae.

***Torynomma (Paratorynomma) dentatum* nov. sp.**

FIGS 10-11, 20

Derivation of name: from the conspicuously dentate fronto-orbital margin.

Material: Holotype P22930 and Paratypes P22931 (Locality 1), P22936, P22941,

P22943 (Loc. 2); P22944 (Loc. 3), P22942 (Loc. 4). Collected by B. Daily 1954.

Localities: South coast of Bathurst Island, north of Darwin, Northern Territory. Beach cliffs and shore platform. Loc. 1-3 are 16-25 km SW of Bathurst Island Mission. Loc. 1: 2.5 km E of Moonkinu Creek, Loc. 2: Meadinga, E of Moonkinu Creek, Loc. 3: Poulmadurie Point, about 4 km E of Moonkinu Creek; Loc. 4: Palliamandera Creek, central south coast, 35 km W of Bathurst Island Mission.

Age: Upper Cenomanian, Bathurst Island Formation, Moonkinu Member, from 3 m above to 5 m below "Tapara Bed" with *Acanthoceras* etc. (see Wright 1963, p.612) at Loc. 1-3. Also from Lower Turonian, upper part of Bathurst Island Formation with *Collignoniceris* cf. *woolghari* (Mantell); Loc. 4. All from glauconitic sands and clays.

Preservation: Most of the 8 specimens examined are exceptionally well preserved and most were almost complete when embedded in the sediment but the shell is in various stages of decortication. The fragile shell and formation of incipient concretions around the bodies, a common feature of the preservation of decapod crustaceans in clays and silts, makes complete preparation difficult. There is little distortion and most specimens show little movement between the carapace and the rest of the body. In several specimens a gap of a few mm between carapace and abdomen and opening of the pleural suture indicates that they are probably moults. Seven specimens are preserved in grey silty clay, one in glauconitic sand. There is no doubt that they lived where they were buried.

Description: Carapace rectangular in outline, wider than long, with a straight fronto-orbital margin; gently convex longitudinally and almost flat transversely. No distinct lateral edge, side walls vertical; posterior margin sinuous. Front projecting only a short distance forward but deflected downward, with median groove and pair of short basal spines. Pointed, conical, supraorbital spine about equidistant from front and conspicuous extraorbital- anterolateral tooth. This is triangular in outline, with flat surface, drawn out into a long, sharp, anterolaterally directed spine. Its anterior margin bears 3-4 small tubercles and its tip is granulated. Surface of carapace uniformly granulated, with only few more prominent tubercles and few smoother areas such

as furrows and surface of anterolateral teeth. Cervical, hepatic and greater part of the branchiocardiac furrows about equally well marked. Another posteriolaterally directed groove connects cervical and branchiocardiac furrows and divides epibranchial lobes. Meso- and metabranchial lobes divided medially by a longitudinal groove extending through the faintly delimited urogastric lobe into the cardiac region. Meso- and metabranchial lobes confluent. Orbits very large and shallow, eyestalks unusually robust with smooth surface. In one specimen a part of what appears to be an antennal stalk projects forward from below the supraorbital tooth for about half the distance separating front from anterolateral tooth. Its proximal portion cannot be freed without damage to the anterior part of the carapace.

The shape of the sternum (Fig. 11) is distinctive. It is generally flat but with sternite 7 (and consequently also 8 which is not preserved) turned upward. All sutures except 1/2 and 4/5 complete and crossing the midline. End of female abdomen extends to a ridge on sternite 4+5. Male abdomen unknown. Gonopores could not be recognised with certainty in this species. A third maxilliped preserved in one specimen shows the elliptical outline of the merus, with subterminal articulation of the carpus. Chelae of the P1 subequal, with elongate rectangular propodus, covered with spiny granulations which tend to be aligned in 2 rows on its upper edge. Fingers as long as the propodus and gently curved. Fixed finger deflexed slightly downward. Merus and carpus spinose, P2 and P3 about equally strong and long, with upper and lower rows of spines on the podomeres. Their length exceeds 20 mm, with a diameter of up to 5 mm. P4 and P5 thin, cylindrical, with a diameter of about 1 mm, smooth, articulated above the bases of the P3.

Dioratiopus Woods, 1953

Type species *D. salebrosus* Woods

- Dioratiopus* Woods, 1953, p. 52; Wright & Collins 1972, p. 33, 34, 42.
Doratiopus Woods, Glaessner 1969, p. R492 (erroneous spelling).
Glaessneria Wright & Collins 1972 (non Takeda & Miyake 1964), p. 34 ff.
Glaessnerella Wright & Collins 1975, p. 441.

As noted by Wright & Collins (1972, p. 33), "the genera *Glaessneria* nov. and *Dioratiopus* Woods are closely allied". The authors state that the species of their new genus are dis-

linguished from the Australian *Dioratopus* by being "much flatter in both transverse and longitudinal section". They "lack the inner oblique sulcus on the mesobranchial area and have more strongly spinose frontal areas". The diagnostic validity of these characters must be questioned. While some of the English species are much flatter than the Australian type species, this is not correct for the European type species "*G.*" *spinosa* (Van Straelen 1936) which is more convex transversely and only insignificantly less so longitudinally, except for the raised sides of its rostrum. The oblique furrow on the branchial area is present in *Dioratopus*, though possibly less pronounced laterally where it joins the branchio-cardiac sulcus. The generally weaker development of carapace furrows in *Dioratopus* cannot be considered as a reliable generic character, and the same applies to the less "spinose frontal areas" which are almost without spines in several European species. Small basal rostral, supraorbital and extra-orbital/anterolateral spines are present in *Dioratopus*. The generic identity of European and Australasian mid-Cretaceous decapod crustaceans is not anomalous but is found in *Homolopsis*, *Notopocorystes* and *Hemioon* among the Brachyura and in Macrura. The species *Homolopsis dawsonensis* Bishop, 1973, which does not have a *linea homolica* was considered by its author to resemble *Homolopsis depressa* Carter but to differ "by being even less ornamented (having no areoles), having a continuous sagittal ridge, having more inflated branchial regions, and a broader cardiac-intestinal region" (Bishop 1973, p. 20). These are specific differences from "*Glaessnerina*" *depressa* which is a *Dioratopus*. Bishop's species extends the range of this genus to the Maastrichtian Pierre Shale of Montana.

Dioratopus salebrosus Woods, 1953

FIG. 12, 12A

Dioratopus salebrosus Woods, 1953, p. 53, pl. 2, fig. 4, 5, text-fig. 2.

Dioratopus salebrosus Woods, Glaessner 1969, p. R492, fig. 304 (2).

Material: One specimen collected and presented by H. Wopfner and D. Scott on behalf of Geosurveys of Australia No. P22933.

Locality: Wooldridge Creek (=Fossil Creek), a tributary of the Alberga River, about 40 km NW of Oodnadatta, South Australia.

Age: Upper Albian, Marree Formation (See N. H. Ludbrook, Bull. 40, Geol. Survey S. Aust., 1966, p. 38, Map 4).

Remarks: The specimen is preserved in part of a hard concretion as an external mould, showing the almost complete carapace and fragmentary pereopods. It agrees completely with the holotype in type in size, shape and ornamentation.

Dioratopus sp.

FIG. 21

Material: One specimen, P22928, collected by B. Daily 1954.

Locality: South coast of Bathurst Island N of Darwin, Northern Territory, Poupanderi Point, about 16 km SW of Bathurst Island Mission.

Age: Upper Cenomanian, Moonkinu Member of Bathurst Island Formation, within about 1 m below the base of the "Tapara Bed".

Preservation: A poorly preserved carapace in a ferruginised concretion containing also scattered remnants and external moulds of pereopods.

Description: Carapace subrectangular, sides slightly converging toward the front. About 21 mm long, 16 mm wide and 7 mm high. Surface gently rising for about 5 mm from base of rostrum, generally flat longitudinally, gently convex transversely. Greatest width appears to be at level of posterior end of cardiac region. Regions of carapace as in type species; spines apparently placed as in *Homolopsis edwardsi* Bell but almost obliterated by erosion and probably originally less prominent. Surface finely granulated. Orbital depressions below the hepatic lobe, smaller than in the type species. Chela with rows of granules on propodus and carpus and with slender, curved dactylus.

This species differs from *H. spinulosa* in some details of outline and in its weaker ornamentation. The specimen is insufficiently preserved for a specific diagnosis but the presence of an additional species in the Bathurst Island Formation is of interest.

Eodorippe nov. gen.

Type species *E. spedeni* nov. sp.

Diagnosis: Characters as described for the type species.

Eodorippe spedeni nov. sp.

FIG. 13, 13A

Derivation of name: After Dr I. Speden, Geological Survey of New Zealand, who sug-

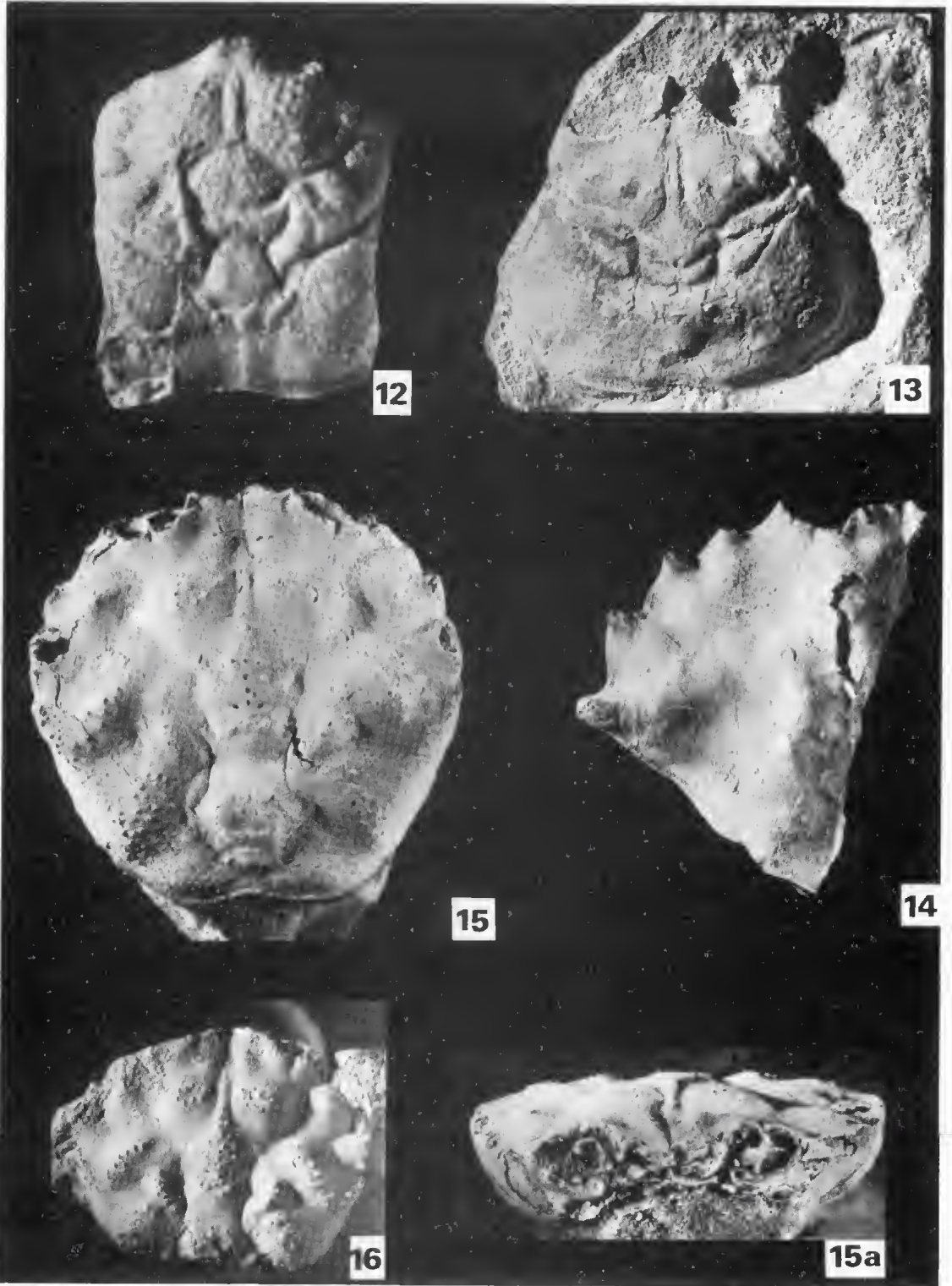


Fig. 12. *Dioratiopus salebrosus* Woods. Artificial cast of carapace of specimen P 22933. x2.
 Fig. 13. *Eodorippe spedeni* nov. sp. x2.
 Fig. 14. *Rhachiosoma granuliferum* (Glaessner). x1.
 Fig. 15, 15a. *Pororaria eocenica* nov. sp. Holotype, 15—dorsal view, 15a—frontal view. x2.
 Fig. 16. *Pororaria eocenica* nov. sp. Paratype DC 361, x2.

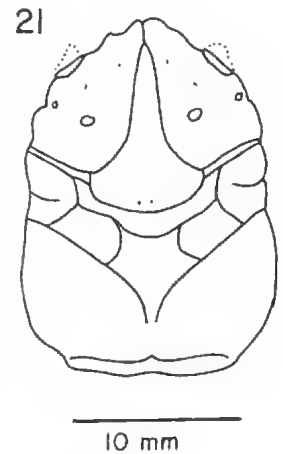
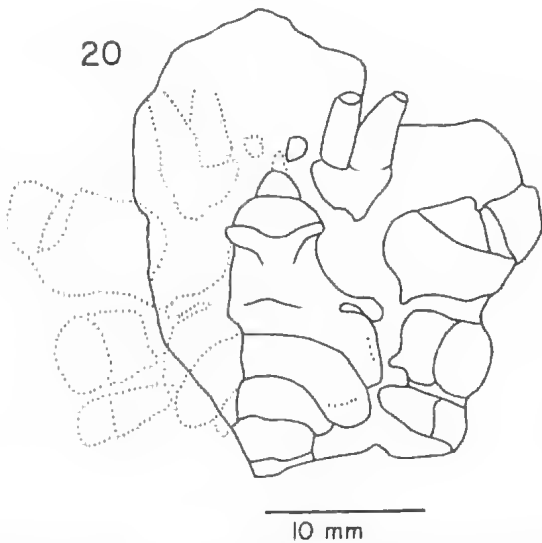
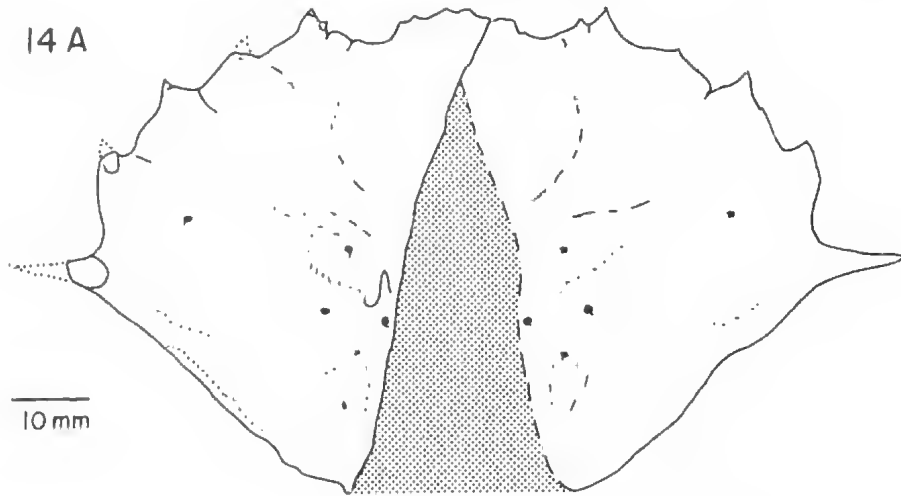


Fig. 14A. *Rachiosoma granuliferum* (Glaessner). Diagrammatic reconstruction of carapace.
 Fig. 20. *Torynomma* (*Paratorynomma*) *dentatum* nov. sp. Paratype P 22936, sternum and appendages, showing tip of mandible, basal parts of Mx3, P 1-3; right side reconstructed in outline.
 Fig. 21. *Dioratipus* sp. Carapace reconstructed.

gested the investigation of specimens from New Zealand and assisted with information.

Material: One specimen, N.Z.G.S., AR 675. Collected by Mrs J. Wiffen.

Locality: Stream boulders from bed of Mangahouanga Stream, a tributary of the Te Hoe River, from between bridge and waterfall. Loc. No. N 104/f 909, Grid ref. N 104/261088.

Age: Campanian-Maastrichtian (Pripauan-Haumurian).

Preservation: Carapace showing dorsal aspect and left flank almost completely preserved, with fragments of shell adhering to surface of internal and partially preserved external mould.

Description: Shell thin, carapace transversely oval in outline, very moderately convex longitudinally and transversely. Greatest width across mesobranchial and cardiac lobes. Rostrum long and narrow, spatulate, pointing forward; small granules on each side of its

base, upper surface with a longitudinal depression, lower surface ridged. Fronto-orbital margin long, transverse. Its inner portion, occupying less than half its width ends laterally in a small, gutter-like depression; outer portion has a smooth, rounded, prominent edge. Infraorbital margin projects beyond upper surface, orbital depressions large and shallow and no suborbital tooth was observed. Extraorbital-anterolateral teeth turn sharply forward, ending in short, pointed spines. Rounded anterolateral margin bears a small hepatic spine and leads to a pronounced sinus in which cervical and branchiocardiac furrows meet, continuing down the flank as a single, straight groove. Behind the incision there is a short, sharp ridge. It begins with a short spine and is directed in an outwardly concave curve backward and outward, slightly above the rounded true lateral carapace periphery. Carapace narrows slightly behind end of ridge. Posterolateral and posterior margins sinuous and marked by a smooth ridge. Concave median part of the posterior margin short. Surface of carapace prominently marked by transverse furrows and a few tubercles. Cervical furrow sinuous and medially interrupted; branchiocardiac furrows straight, convergent but become unclear near the cardiac region. Between cervical and branchiocardiac furrows a pair of intermediate oblique grooves are the most distinctive character of this carapace pattern. They are lateral extensions of a groove between the meso- and metagastric lobes which are bisected by a weaker median (longitudinal) furrow. Anterior and posterior portions of the dorsal surface are undivided by grooves and are convex on each side. Proto-gastric lobes bear three tubercles each, spaced about equally along an arc in front of the cervical groove, leading to hepatic spine. Mesogastric lobe, bounded by straight lines, extends a long and very narrow tongue forward. An elongate anterior and a shorter posterior epibranchial lobe on each side, the anterior ending in a small marginal tubercle in the junction of the main transverse grooves, the posterior is shorter, obliquely triangular in outline, and sharply delimited from the metagastric lobe. A faint, medially interrupted, transverse ridge and some granulation on the anterior part of the ill-defined cardiac region. Surface minutely granulated, with some coarser granules on the mesobranchial lobes.

Remarks: There are some similarities in shape of the carapace and the orbits between

the new species and *Mithracites vectensis* Gould from the Lower Aptian of England. The differences in the pattern of the transverse furrows, the shape of the mesogastric lobe, the narrow rostrum and the lack of the coarse ornamentation in *Eodorippe* justify a generic distinction.

Systematic position: Withers (1951) placed *Mithracites* in the Prosopidae, a view rightly criticised by Wright & Collins (1972, p. 40). They point with some justification to certain similarities with "*Glaessneria*", here placed in the synonymy of *Dioratiopus*, and consequently include it in the family Cymonomidae. The Late Cretaceous new genus has some similarities with Cymonominae. The lack of information on the morphology of the ventral side of the cephalothorax of *Eodorippe* makes its placing in a modern classification difficult. In the absence of more complete specimens we cannot decide whether this new genus is peditrete or sternitrete and whether it is oxystomatous. Despite the absence of such information the striking resemblance between the carapace of *Eodorippe* and the genus *Dorippe* cannot be disregarded. It is seen not only in trivial generalities of shape and ornamentation which can be due to common convergences but in details which are unique and cannot be dismissed. The sinuosity of the wide posterior-posterolateral margin can be interpreted as indicating a position of the third and fifth pereopods similar to that in *Dorippe* (the bases of the third pereopods do not affect the shape of the carapace margin). The lateral convergence of the cervical and branchiocardiac grooves resembles closely the pattern in several species of *Dorippe* (*D. facchino* Herbst, *D. japonica* von Siebold, *D. granulata* de Haan) while the intermediate transverse groove appears to be present in *D. dorsipes*. The position and shape of the shallow orbits, the divided supraorbital margin and the extra-orbital teeth are also similar. If the classification of Guinot (1978) is followed and the Palicidae are placed with the Dorippoidea, some resemblances between *Eodorippe* and *Pulcus* Philippi, 1838 become significant: the great width across the mesobranchial lobes, the unusual multiplication of the transverse grooves, and the development of a sagittal mesogastric and metagastric furrow. Significant differences are the apparent absence of the prominent infraorbital teeth of *Dorippe* and the shape of the rostrum. This shape makes it unlikely that *Eodorippe* had reached the oxy-

stomatous condition of *Dorippe* with its dorsally visible exhalent opening. It agrees with this structure in the Tymolidae and Tornyomidae. The known characters of *Eodorippe* suggest a derivation of the Dorippoidea from Tymoloidea. This hypothesis remains to be tested by a study of the still unknown ventral structures of the cephalothorax of *Eodorippe*. It is tentatively attached to the Family Tornyomidae.

Family Portunidae

Rhachiosoma granuliferum (Glaessner, 1960)

FIG. 14, 14A

Portunites granulifer Glaessner 1960, p. 21, pl. 3, fig. 7, text fig. 9.

New locality: Coastal cliff at Pororari, 2.4 km N of Punakaiki, Grid ref. S37/723, c852318.

Material and preservation: The incomplete left half of a carapace, broken from the right half of the front to the posterior margin above the fifth left pereopod. The anterolateral teeth 2-5 are damaged. Most of the shell surface is preserved. Canterbury Museum, Christchurch, New Zealand, No. zfc 9, coll. R. S. Allen, Feb. 1935.

Age: Upper Eocene, Kaiatan-Runangan. The holotype was from the Middle Eocene.

Remarks: Further studies of the type species of *Portunites* (*P. incertus* Bell) suggest that the original generic assignment of the species *granulifera* was inappropriate. Prominent lateral spines are equal to almost half the width of the carapace in *Rhachiosoma bispinosum* Woodward, 1871 from the Lower Eocene London Clay, but less than a quarter of that width in *R. granulifera*. However, the orbits and carapace sculpture are similar. The new, fragmentary specimen has weaker and probably fewer tubercles on the carapace surface than the holotype but until new and more complete material is found, these differences are insufficient for the establishment of a new taxon. The classification of these fossils should be reviewed when the ventral aspect and pereopods are known.

Family uncertain

Pororaria nov. gen.

Type species *P. cocenica* nov. sp.

Diagnosis: Characters as described for the type species.

Pororaria cocenica sp. nov.

FIGS 15, 15, 16

Material: Two almost complete carapaces. Holotype (including right chela). New Zealand Geological Survey collection DC 360, paratype DC 361. Also fragments of carapaces, chelae and walking legs and one carapace with both chelae. Canterbury Museum, Christchurch, New Zealand, No. zfc 31-38, coll. R. S. Allen Feb. 1935.

Locality: Cliffs at Pororari, 2.4 km N of Perpendicular Point, Punakaiki (zfc 31-38); 800 m S of Perpendicular Point, Map Sheet S 37/735, N.Z. Geol. Survey locality GS 10490 (DC 360-361).

Age: Upper Eocene, Kaiatan-Runangan.

Description: Carapace as long as wide, outline oval to hexagonal, very slightly convex to flat surface smooth with localised concentrations of granules. Front with a median notch and on each side 1 strong and 2 weak teeth. Orbits as wide as the front, with supra-orbital granulations and 2 notches, with a gap between the large antennal base and an infra-orbital tooth. Antennular bases folded back obliquely. About 5 anterolateral teeth, obscured by marginal granulations. Posterolateral margin starts from a ridge behind last lateral tooth but not delineated on the inflated meso-branchial lobes. Cervical groove well defined, starting from postero-gastric pits and delimiting on each side in three forwardly concave arcs the mesogastric, proto-gastric and hepatic lobes. These are equally well defined by hepatic grooves. There are conical tubercles on hepatic lobes; groups of spinose granules on meso-, proto- and metagastric, epi-, meso- and metabranchial, and cardiac lobes. Epi-branchial field of granules has an unusual U-shape which resembles similarly placed granulations in *Dakotacancer* Rathbun. As in this genus, a branchiocardiac groove crosses rounded lateral margin behind this granulated lobe. Urogastric lobe finely pitted and rectangular, cardiac region broadly hexagonal. Posterior margin has a strong, granulated ridge with a slight median forward bend. Chelipeds are strong and heterochelous. Carpus with spine near its inner distal angle. Inflated propodus has smooth inner and granulated outer and upper surfaces. Granules tend to be arranged in longitudinal rows. Fingers shorter than the upper length of the propodus, strong, minutely granulated, grooved

but otherwise smooth. Walking legs preserved as scattered fragments which are thin and long.

Systematic position: In the absence of complete pereopods and of the sternum it is difficult to reach a definite conclusion about the assignment of this new genus to an existing higher taxon. It resembles the less advanced Portunidae such as some Carcininae (*Nectocarcinus*, *Carcinus*) in the general shape of the carapace and in some characters of its fronto-orbital region. *Nectocarcinus* shows a similar transition from anterolateral teeth to groups of spiny granules. The chelipeds are also similar. Thin, long legs do not occur in Carcininae and the lobes of the posterior half of the carapace are different. There are also resemblances with Atelecyclidae among the Corystoidea but the relevant details of the fronto-orbital region are not well enough preserved in the genus to allow a definite conclusion about portunoid or corystoid affinities; the configuration of the postero-lateral portion of the carapace does not favour the latter but the chelae are cancrroid. A similarity of the carapace with that of *Avitelmessus* Rathbun does not apply to its median portion which shows a corystoid pattern. *Avitelmessus* is very close to *Dakoticancer*. As Guinot (1978) remarked, these genera should not be assigned to the Dromioidea. Whether *Pororaria* is related to Corystoidea or Portunoidea remains to be elucidated. Until further evidence is found, the new genus is tentatively placed in the superfamily Portunoidea.

Family Panopeidae

Panopeus H. Milne Edwards, 1843

Type species *P. herbsti* H. Milne Edwards

Panopeus whittenensis nov. sp.

FIGS 17-19

Material: More or less complete carapaces, chelae, fingers, and fragments of legs. Holotype P22935, paratypes P22938, 22939, 22946-22950.

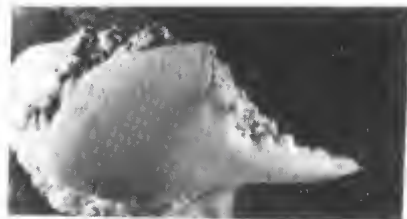
Localities: Whitten Bluff, S of Christies Beach, 28 km SSW of Adelaide (type locality and most common occurrence). Also from



17



18



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Fig. 17. *Panopeus whittenensis* nov. sp. Holotype, x3. Posterolateral margins restored.

Fig. 18. *Panopeus whittenensis* nov. sp. Paratype P 22938, x2.

Fig. 19. *Panopeus whittenensis* nov. sp. Right chela, specimen P 22939, x2.

Maslin Bay, about 15 km further south. Coastal cliffs on the E shore of Gulf St Vincent (P22938, coll. Dr M. Buonaiuto).

Age: Upper Eocene, upper Tortachilla Limestone and base of Blanche Point Formation (= "Transitional Marl"). Planktonic foraminiferal zone 15.

Preservation: Some complete and some broken carapaces without branchiostegites, sternum, abdomen, or attached appendages. The propodus of the cheliped may have the dactylus and parts of the carpus attached but more often it is disjointed. Small fragments of pereopods apparently belong to this species. The only other decapods found with *Panopeus*, in a rich shallow-water fauna of cirripeds, bryozoans, brachiopods, echinoderms, serpulid worm tubes (some attached to carapaces and claws of *Panopeus*) and numerous mollusca are one incomplete dromiid carapace (*Dromiites?* sp.), a few claws of an oxyrhynchous crab, and chelae of a callinassid.

Description: Carapace slightly wider than long, convex. Frontal margin straight, with median indentation and transversely grooved and finely granulated edge. Orbits well developed, with inner supra- and infraorbital teeth, evenly granulated edges and 2 supra-orbital fissures. Anterolateral margins with 5 conical teeth of which the fourth is the strongest and most prominent and the fifth the weakest. Posterolateral margins converging backward. Posterior margin wide, with raised, faintly granulated rim. Main regions of the carapace surface well marked by shallow grooves. Posterior gastric pits clearly visible. Surface appears to be smooth when well preserved, becoming granulated with decortication by weathering. Some individual variability in ornamentation. No remarkable features in the pattern of regions except perhaps strong development of the epigastric and metagastric lobes. Right chela strong, propodus smooth, with a very faint depression below the upper edge and two rows of pits above and along lower edge of fixed finger. A row of irregularly sized and blunt teeth on its upper edge. Lower edge of the propodus and finger strongly curved to fit snugly along the anterior margin cephalothorax. The carpus is square.

Measurements (in mm): Lengths and widths 17.8 and 22.5, 22 and 26, 20.5 and 23, 22.5 and 28. In the carapace which is 20.5 mm long, the frontal margin has a half-width of 4 mm and the orbit was 4.5 mm wide. In a cara-

pace which was about 20 mm long and 24 mm wide, the orbit was about 5 mm wide. A large propodus with fixed finger is about 35 mm long and 18 mm high.

Remarks: In the absence of any parts of the ventral surface of the cephalothorax or appendages other than the large claw, the precise systematic position of this crab remains in some doubt. The absence of transverse raised lines on the carapace would distinguish it from the living species of *Panopeus* for which their presence is a convenient diagnostic character. It would not necessarily exclude it from the evolutionary lineage of this genus which has been reported from the Paleocene and Eocene. The new species as far as known, is morphologically closest to *Panopeus* and therefore assigned to it, pending discovery of other still missing parts.

Phylogenetic conclusions

The phylogenetic significance of several of the new Cretaceous and Tertiary crabs here described has been briefly mentioned. It can now be considered in the framework of the adaptive radiation of the Brachyura (Fig. 22, see also Glaessner 1980). This updated version of a phylogenetic diagram which I first published 50 years ago (Glaessner 1930; 1960, Fig. 22) incorporates some of the results of the monographic work of Wright & Collins (1972) on British Lower Cretaceous crabs and reflects the new classification of the Brachyura by Guinot (1977, 1978) and other important studies which are considered in it. Certain modifications and re-arrangements of this classification are suggested as a result of the present investigation.

The new family Torynommidae may have evolved ultimately from the family Prosopidae of the Homolodromioidea, as implied by Wright & Collins (1972) and probably from archaobrachyuran descendants, the Homoloidea, in Late Jurassic-Early Cretaceous or in Mid-Cretaceous time. Their living descendants are related to them in a manner depicted with remarkable foresight by Bouvier as early as 1897. They also may have given rise to the Late Cretaceous Carcineritidae which acquired an early adaptation to swimming. From similar origins in the podotrematous Homoloidea the well documented Necrocarcininae-Calappinae lineage (Förster 1968) and possibly Orithyidae (see Guinot 1978, p.255) evolved and eventually attained the heterotrematous grade. Their Mid-Cretaceous descendants, the

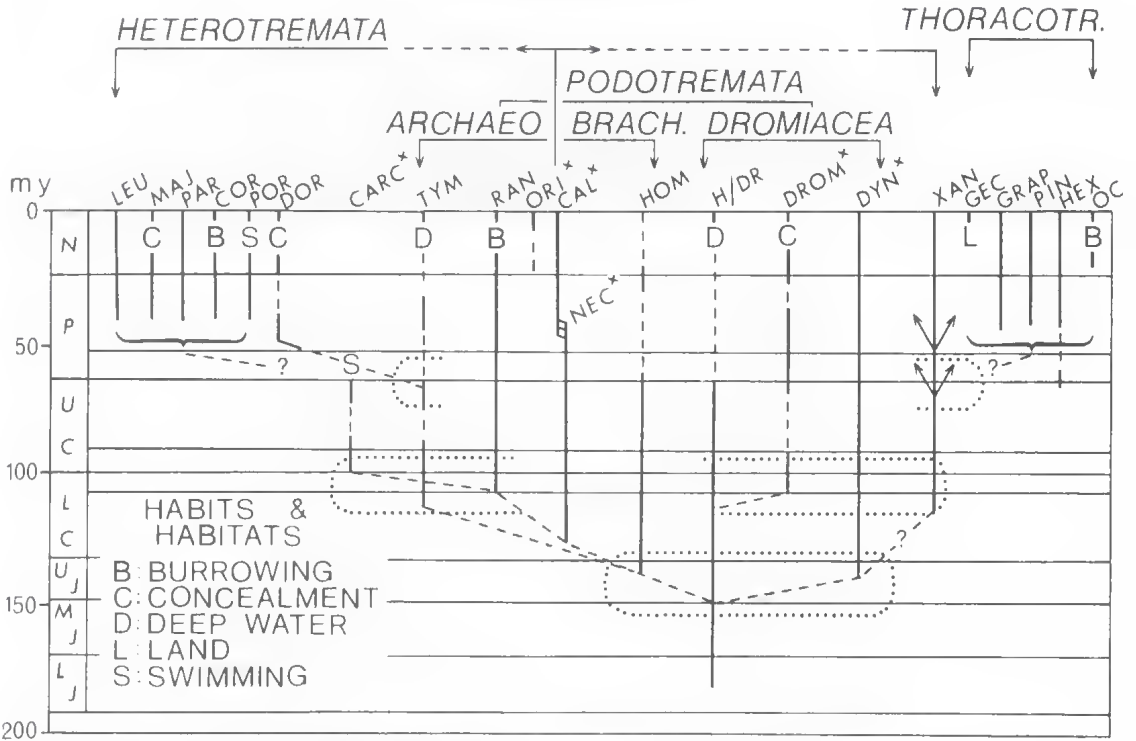


Fig. 22. Adaptive radiation of the Brachyura.

Superfamilies (and lower taxa marked with *): LEU Leucosioidea, MAJ Majoidea, PAR Parthenopoidea, COR Crystoidea, POR Portunoidea, DOR Dorippoidea, CARC* Carcineretidae, TYM Tymoloidea, RAN Raninoidea, ORI* Orithyidae, CAL* Calappidae, NEC* Necrocarcininae, HOM Homoloidea, H/DR Homolodromioidea, DROM* Dromiidae, DYN* Dynomenidae, XAN Xanthoidea, GEC Gecarcinoidea, GRAP Grapsoidea, PIN Pinnotheroidea, HEX Hexapodoidea, OC Ocypodoidea. Geochronometric (in million years, my) and stratigraphic scales at left. N Neogene, P Palaeogene, UC Upper Cretaceous, LC Lower Cretaceous, UJ Upper Jurassic, MJ Middle Jurassic, LJ Lower Jurassic. Note that top of Paleocene is shown within Palaeogene, and Albian and Cenomanian are marked below and above line dividing Cretaceous. Dotted lines mark the three periods of major diversification of the Brachyura.

Raninidae, adapted to burrowing and remained at the podotrematous grade. The discovery of *Eodorippe* strongly suggests a Late Cretaceous origination of the heterotrematous Dorippidae from Tymoloidea, as foreseen by Bouvier. This is still subject to confirmation by more complete material.

The origins of the remaining Heterotremata are still unknown, probably diverse, and dated mostly Late Cretaceous to Early Tertiary. Wright & Collins (1972) conclude that the Xanthidae were derived from Dynomenidae in Late Jurassic-Early Cretaceous time. This derivation cannot apply to other Heterotremata which show no signs of origination from Dromiacea or indeed of pre-Tertiary existence. It is possible that further studies of *Pororaria* may clarify relations with or between Portunoidea and/or Crystoidea (a prior synonym of Cancriformia). Some members of these two superfamilies show a dichotomy between

habits and adaptations for swimming (as in *Portunus*) as opposed to burrowing (as in *Crystes*). The portunoid adaptations for swimming do not seem to be derived from but rather heterochronously convergent to those of the Carcineretidae. The burrowing habit of the Crystidae is generally considered as a convergent or possibly parallel adaptation compared with that of the Raninidae. The origins of the Leucosioidea and Majoidea remain obscure; their adaptations diverge distinctively from those of any other group of crabs.

The Thoracotremata, at the highest grade, include the land crabs and various successful strand dwellers with a variety of habits. They resemble the Xanthoidea more than other Heterotremata but their origin, in the Late Cretaceous or Early Tertiary, is cryptic.

As in all phylogenies, many questions remain, but new material, particularly of Mesozoic and Early Tertiary age, can now be

fitted more easily and rationally into the framework of existing knowledge and classification. Most importantly, the replacement of the traditional but mostly ill-conceived "Sections" with a horizontal classification at the highest level by grades, has improved our understanding of the history of the Brachyura.

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All specimens with numbers prefixed P have been deposited in the South Australian Museum, Adelaide. The photographs were prepared by Mr R. Barrett. The skilful drafting of Fig. 22 is the work of Miss A. M. C. Swan, Geology Department, University of Adelaide.

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Postscript

Via Boada (1980) reviewed the evolution of the Ocypodoidea, tracing their origin to the Cretaceous genera *Ophihalmoplax* and *Archaeopus*. I had previously (Glaessner 1969) referred the first to the Carcineretidae and the second, doubtfully, to the Palicidae. Subject to further studies, Via's views suggest interesting possibilities of exploring evolutionary links between Ocypodoidea, certain Dorippoidea, and Carcineretidae. When I received

his new data it became possible to identify a Middle to Late Eocene crab from a limestone core from the Ashmore Reef No. 1 Bore off the NW coast of Australia (sent to me in 1968 by Dr P. J. Coleman and the Burmah Oil Company) as at least very close to *Retropluma* as described from rocks of similar age in Spain. It lives now in deep water in the Indian Ocean.